

UNI
8128

HARVARD UNIVERSITY



Library of the
Museum of
Comparative Zoology

5-NA-[Lawrence]

OCCASIONAL PAPERS

of the MUSEUM OF NATURAL HISTORY The University of Kansas Lawrence, Kansas

NUMBER 50, PAGES 1-21

APRIL 15, 1976

SEXUAL SIZE DIFFERENCES IN THE MAINLAND ANOLES

By

HENRY S. FITCH¹

In several seasons of field work in Mexico and Central America during which many species of *Anolis* were observed, the writer became impressed with the ecologic and morphologic diversity within this large genus. Especially, it became evident that the relative sizes of males and females vary much more than has been realized, from species having relatively very large males to those having very large females. The objective of the present study was to confirm the existence of such differences, to measure them, and to seek possible causes and correlations.

Disparity in size between the sexes is a common phenomenon in vertebrates. Most frequently males are larger than females, but in some species females may approximate the sizes of males, and in others may be larger than the male. Relatively large size in males is characteristically related to behavior in which there is active aggression and competition for mates. In polygynous animals the disparity in size may be extreme, with males attaining several times the bulk of females. In certain groups, including raptorial birds and many kinds of snakes, females are normally larger. The relatively large females of such predators often are aggressive and dominant and in the males territoriality and aggression are weakly developed or absent.

Iguanids and lizards of a few other families differ from the majority of squamate reptiles in being visually oriented, both in finding food and in interacting with other members of their species (Evans, 1965). Bright colors and display organs associated with them are usually well developed in males, but are poorly developed

¹ Museum of Natural History and Department of Systematics and Ecology, The University of Kansas, Lawrence, Kansas 66045.

or absent in females. Iguanid males have general coloration brighter than that of females and both sexes have considerable capacity for modifying their colors. A male that is cold and inactive, or fleeing from recent defeat by a rival, is much different in appearance from one engaged in active aggression. Sexual dimorphism in iguanids also involves differences in size and proportions. Usually males are larger, have relatively large heads with swollen jowls resulting from enlarged jaw musculature, and have longer tails. In some instances in which the sexes are of approximately equal size (*Phrynosoma*), and especially in instances in which the female is markedly larger (*Crotaphytus wislizenii*), territoriality and male aggression are absent or only weakly developed.

In *Anolis*, species confined to small islands with no sympatric congeners have been found to show marked size disparity between the sexes, resulting in decreased competition for food and other resources. On larger islands, having several or many sympatric species, the sexual difference in size is less because the interspecific competition of larger and/or smaller species constrains intraspecific size divergence of the sexes (Schoener, 1967, 1968; Williams, 1969).

METHODS AND MATERIALS

In the course of demographic studies of anoles in Costa Rica at Beverly, Boca de Barranca, Hacienda El Prado, La Irma, Sardinal, San José and Turrialba (1967-70) and at Finca La Selva, Monteverde and Finca Las Cruces (1973-74), I captured and measured large series in year-round samples of various species. The lizards were measured alive, marked and released. In the course of field work in Guatemala (1971) and southern Mexico (1972-73) and Ecuador (1975) series of numerous additional species were collected and measurements were made either while the lizards were alive, or when they were freshly killed and relaxed just before preservation.

Samples of other species were obtained from the specimens in the University of Kansas Museum of Natural History collection. Preserved specimens harden and shrink by several per cent, and obviously their measurements are not strictly comparable with those of live animals. To keep measurement error to a minimum the series used for each species consisted either of fresh material or preserved material.

Only the snout-vent measurement was used in comparing the sexes. The lizards, whether alive or preserved, were straightened with the fingers, moderately stretched with gentle pressure, and held against a plastic ruler for measurement to the nearest millimeter.

Most series measured included individuals that were considered to be immature and were therefore excluded from computations of mean lengths in adult males and females. Decisions concerning the minimum size of individuals to be included were somewhat sub-

jective. In females the presence of enlarged ovarian follicles or oviducal eggs was the best criterion, but the stage of development of follicles or even their presence could not always be determined in the live anoles marked and released, and in series of preserved specimens collected at the time of year when reproduction had ceased, this criterion did not apply. Occasional unusually precocious females ovulate at a size when most are still sexually immature; inclusion of all those in a given size-class on the basis of one precocious individual would result in some bias, with depression of the mean.

In males, minimum adult size was even more difficult to establish. One obvious criterion, the production of mature sperm, was difficult to determine in preserved material and even in live anoles in the field. In any case production of sperm may be achieved while the lizard is still in an early stage of growth and is immature by other standards. In the absence of adult males, juveniles in another kind of iguanid, *Crotaphytus collaris*, were found not only to produce sperm but to be successful in fecundating adult females of approximately ten times their own bulk (Fitch, 1956). Therefore, in the present study, production of sperm was rejected as a criterion of maturity.

In both male and female anoles, adult snout-vent length measurements tended to form a curve with few individuals near the maximum size, largest numbers in the intermediate size classes near the average, and decreasing numbers in the size classes of small adults, in which, presumably, growth was still fairly rapid. The one-millimeter size range containing the largest number of individuals often included or approximated the mean. The most numerous size class of adults was usually about ten per cent below the maximum size in those species represented by adequate series. Smaller individuals were also included down to a group ten per cent smaller than the average or modal adult size.

Departure from a normal distribution in adult size resulted from the fact that growth continues after adulthood is attained, but at a slower rate than in young, and at a slower rate in large, old adults than in relatively small young adults. Of the anoles that reach maturity many are eliminated before they reach average adult size and relatively few attain maximum size. Therefore, the distribution of adult sizes is skewed, with relatively large numbers of young adults depressing the mean somewhat.

Composition of the population varied in each species sample obtained. In some samples there was a high proportion of immatures, whereas in other samples young were scarce or absent, depending partly on the area and the season. At the beginning of a breeding season field samples might consist mostly of fully grown adults, and several months later the samples might contain a high proportion of newly matured, small adults.

TABLE 1.—SIZE RELATIONSHIPS OF THE SEXES IN 54 POPULATIONS OF MAINLAND ANOLES.

Species or population	Percentage female-to-male length	MALE				FEMALE			
		N	Snout-Vent Mean	Length Standard error	Range	N	Snout-Vent Mean	Length Standard error	Range
aequatorialis	97.31	7	82.2	±2.02	88-71	3	80.0	±2.06	83-75
aquaticus	88.770°°	10	65.9	±1.47	71-57	9	58.55	±.97	62-59
attenuatus	95.384	24	84.5	±1.62	95-78	18	80.6	±1.02	90-74
auratus	104.484°	31	44.6	±.448	49-40	8	46.6	±.726	49-43
biporcatus	101.95	24	87.0	±1.24	98-73	19	88.7	±1.08	97-77
biscutiger	105.63°°	42	37.3	±.332	43-33	33	39.4	±.416	44-36
bourgaei	103.113	24	54.6	±.716	61-47	13	56.3	±.76	65-46
capito	106.413°	13	84.2	±1.01	90-78	13	89.6	±1.11	96-83
carolinensis	78.964°°	14	59.9	±.962	66-54	12	47.3	±1.20	53-41
carpenteri	104.935	6	38.5	±1.32	41-35	14	40.4	±.771	45-36
chrysolepis	104.55	29	71.5	±.548	79-66	32	74.4	±1.26	80-67
crassulus	88.405	8	48.3	±1.74	53-39	7	42.7	±2.54	56-35
cupreus (cupreus)	87.974°°	233	47.4	±.164	53-41	239	41.7	±.164	48-37
cupreus (hoffmanni)	96.598°°	314	44.1	±.196	52-38	166	42.6	±.335	51-38
cupreus (macrophallus)	82.258°°	53	49.6	±.432	54-43	33	40.8	±.490	46-34
cupreus (spilomelas)	84.072°°	57	49.6	±.467	55-41	23	41.7	±.832	49-36
cuprinus	73.459°°	22	63.3	±.638	69-58	15	46.5	±.800	53-42
damulus	110.218°	9	43.1	±.98	48-37	12	47.5	±1.04	52-41
dollfusianus	94.102°°	54	39.0	±.26	43-35	42	36.7	±.530	40-32
dumii	83.302°	3	53.4	±1.90	58-53	6	44.7	±.99	48-42
frenatus	82.250°°	15	132.4	±1.04	143-121	20	108.9	±.96	118-100
fuscoauratus	107.852°°	12	42.0	±.351	43-39	12	45.3	±.660	50-40
gadovii	88.668°°	10	70.6	±1.69	76-62	12	62.6	±.97	69-56
gemmosus	93.600°°	38	62.5	±.352	66-58	28	58.5	±.347	63-56
heteropholidotus	109.259°	10	48.6	±.55	51-45	7	53.1	±.99	58-49
humilis	104.904°°	155	36.7	±.161	43-32	106	38.5	±.195	43-34

intermedius	98.913	241	46.0	$\pm .228$	54-39	98	45.5	$\pm .372$	53-39
kenptoni	104.375*	13	48.0	$\pm .645$	53-45	21	50.1	$\pm .471$	54-46
lemurinus	103.880	13	67.0	± 1.66	79-59	16	69.6	± 1.28	78-59
limifrons (Panama)	98.519	10	43.9	$\pm .81$	48-38	8	43.25	$\pm .364$	46-41
limifrons (Turrialba)	102.93**	392	37.5	$\pm .095$	43-33	276	38.6	$\pm .335$	45-34
lionotus	84.755**	19	71.5	$\pm .854$	78-65	24	60.6	$\pm .725$	68-56
megapholidotus	97.807	28	45.6	$\pm .565$	53-41	14	44.6	$\pm .641$	49-35
nebulosus	100.00	58	42.0	$\pm .422$	49-35	44	42.0	$\pm .478$	49-35
nigrolineatus	94.302**	14	50.9	$\pm .488$	55-47	15	48.0	$\pm .390$	51-45
ortoni	95.726	9	46.8	± 1.14	54-43	8	44.8	$\pm .688$	48-42
pachypus	101.098	32	45.5	$\pm .43$	50-40	24	46.0	$\pm .523$	50-41
pentapion	80.862**	5	74.2	± 1.47	79-70	5	60.0	$\pm .849$	63-57
peracae	92.785**	21	49.9	$\pm .373$	52-46	9	46.3	$\pm .500$	48-44
petersi	100.712	3	98.3	± 1.31	102-96	4	99.0	± 3.07	108-91
poecilopus	96.062	8	63.5	± 1.80	72-56	9	61.0	± 1.14	68-56
polylepis	92.927**	40	50.9	$\pm .435$	57-45	48	47.3	$\pm .264$	53-41
punctatus	88.198**	4	80.5	$\pm .830$	83-79	12	71.5	± 1.21	77-64
rodriguezi	100.92	15	43.3	$\pm .531$	46-40	23	43.7	$\pm .484$	49-40
sericeus	90.308**	47	45.4	$\pm .440$	52-40	34	41.0	$\pm .355$	47-36
subocularis	76.078**	49	51.0	$\pm .529$	63-44	19	38.8	± 1.05	48-33
taylori	79.387**	45	71.8	$\pm .39$	78-64	21	57.0	$\pm .82$	64-53
trachyderma	115.315**	129	44.4	$\pm .214$	52-38	101	51.2	$\pm .482$	57-46
tropidogaster	96.00	24	50.0	$\pm .553$	55-43	15	48.0	$\pm .763$	54-43
tropidolepis	99.01	298	50.6	$\pm .189$	59-43	175	50.1	$\pm .253$	58-43
tropidonotus	81.070**	16	52.3	$\pm .805$	55-46	34	42.4	$\pm .719$	53-36
uniformis	98.128	29	37.4	$\pm .402$	40-35	13	36.7	$\pm .349$	38-34
vittigerus	125.420**	7	52.28	± 1.62	57-45	7	65.57	± 1.155	70-60
woodi	86.617*	4	80.75	± 1.68	87-78	10	69.9	± 1.69	77-61

* Significant dimorphism assumed where $P \leq 0.05$ (one asterisk); two asterisks indicates $P \leq 0.01$.

Comparisons among the 54 populations studied were limited because published information concerning ecological traits, size, and display organs is meager. Most such information had to be obtained from field observations. Field notes on file in the University of Kansas Museum of Natural History provided information about habitat, perch height, size and color of dewlap, and other items for those species I studied from museum specimens without seeing them in life. The field notes of Dr. William E. Duellman were especially useful in providing such bits of information.

To determine what factors control sexual size differences, the 54 populations studied were grouped in several assemblages on the following bases: (1) Geographical distribution (North America including Mexico west of the Isthmus of Tehuantepec, Central America, and northern South America are well-defined faunal areas). (2) Phylogeny (major natural divisions within the genus are the Alpha and Beta sections, with comparable numbers of species in each and considered by some taxonomists to be distinct genera). (3) Size, as reflected by snout-vent length (sequence of rank would differ somewhat depending whether adult male size, adult female size, or a combination were used). (4) Habits, especially with respect to height of perch (the series include some species that are highly arboreal, some that tend to stay on tree trunks or low trees, some that are tree-trunk-to-ground oriented and some that live at ground level, in leaf litter, grass, or rocky riparian habitat). (5) Development of a dewlap, the male display organ (whether large, medium or small, whether bearing contrasting markings or not, and whether having two or more bright colors, one color, or dull and relatively colorless); a related problem is the presence of a dewlap in the female—in most kinds it is absent, but in some the throat is colored like the male's dewlap, in others there is a diminutive replica of the dewlap, and in still others, it approaches the size of the male's organ. (6) Co-occurrence with other species, in sympatry, or more intimately in syntopy, with inter-specific competition, especially between individuals of nearly the same size, providing selective pressure that could affect intraspecific size relationships between the sexes. (7) Seasonality in climate imposing concentrated reproductive and territorial activity, as contrasted with a uniform and favorable climate permitting even distribution of reproductive and territorial activity throughout the year.

RESULTS

Variation in sexual size difference.—The 54 anole populations tested showed a remarkably wide range of size relationships between the sexes (see Table 1), with female-to-male ratio varying from a minimum of 73.5% (*cuprinus*) to a maximum of 125.4% (*vittigerus*). Between the ratios of 79% and 110% the species formed a

virtual continuum; species outside this range, which had relatively large males, were *cuprinus*, and *subocularis* (76.1%), and those which had relatively large females were *vittigerus* and *trachyderma* (115.3%). In 63% of the 54 populations sampled, males were larger, in 35% females were larger, and in just one population (2%) there was no discernible size difference. Greatest concentration of kinds (nine populations) was in the narrow range of 98% to 102%, with males and females of approximately equal size.

It is noteworthy that species having sexual difference of not more than 10% are evenly distributed between those with the male larger and those with the female larger, but among the kinds found to have a difference of from more than 10% to 20% there are 13 populations with larger males and only one population with larger females. Likewise, among kinds having differences of from more than 20% up to 30% there are four species having the male larger and only one in which the female is larger.

For the combined sample of 54 populations males averaged 4.62%



FIG. 1.—Left: displaying male (above) and female of *Anolis cuprinus*, showing relatively large size of male. Right: displaying male (above) and female of *Anolis vittigerus*, showing relatively large size of female.

larger than females. Difference in length between the sexes averaged 10.48% (10.52% in those having the male larger and 5.70% in those having the female larger).

Significance of correlations.—Departures from parity in female-male size ratios in both directions and in varying degrees, have provided some of the most obvious and striking differences among the species of *Anolis*. This dimorphism might be expected to show a high degree of correlation with ecological traits, revealing evolutionary trends. In a search for such correlations, various morphological, geographical, and behavioral characteristics were subjected to various non-parametric biometrical tests as shown in Table 2. All tests used are described by Sokol and Rohlf (1969). Ranking of species and their alignment in the contrasting groups that were the basis for the tests, are listed in Appendix 2.

Several characters including dewlap color, perch height, and female size, showed no significant correlation with sexual difference in size. Other characters, including phylogenetic relationships, with

TABLE 2.—TRAITS OF 54 *Anolis* SPECIES TESTED FOR CORRELATION WITH SEXUAL DIFFERENCES IN SIZE

Trait Tested	Type of Test	Basis For Partitioning Sample ¹	Calculated Value
Female dewlap	Kruskal-Wallis	medium or large small absent, throat colored absent, throat plain	$H = 7.2965$
Phylogeny	Kruskal-Wallis	3 groups of Betas	$H = 7.7842$
Phylogeny	Wilcoxon 2-sample	Alphas vs. Betas	$C = 2.1109^*$
Geography	Kruskal-Wallis	N. America Cent. America S. America	$H = 5.87585$
Dewlap size	Kruskal-Wallis	large medium small	$H = 18.96^{**}$
Dewlap color	Kruskal-Wallis	2 or more colors 1 color no bright colors	$H = 2.41$
Habits (Perch height)	Kruskal-Wallis	arboreal (high) arboreal (low) trunk to ground ground level	$H = 1.56$
Co-occurrence or isolation	Kruskal-Wallis	widespread-dominant restricted and dominated marginal and isolated	$H = 9.0598^*$
Female size	Kendall coefficient of rank correlation		$\tau = .4547$

¹ See Appendix 2.

*, $P \leq .05$; **, $P \leq .001$.

dichotomy of Alpha and Beta anoles, dewlap size, and degree of co-occurrence or isolation, showed significant correlations, and still other characters, including relationship within the Beta anoles, development of female dewlap, and geographical distribution, approached a minimum level of significance.

Relatively large size in the male was found to be highly correlated with relatively large dewlap size; this is not surprising, because both can be expected in kinds of anoles that have male aggression highly developed and are territorial and/or polygynous. However, it was rather surprising that dewlap color did not show similar correlation. Presumably, a brightly colored dewlap is a more effective display organ than one which is dull white, gray or brown, and a dewlap with several contrasting colors is more effective than one of uniform coloration.

Geography and phylogeny are obviously correlated. The nine North American species included are all marginal to the range of the genus, and are either isolated or have relatively few sympatric species, and in this respect they may be comparable with insular populations; males average 12.4% larger than females, as contrasted with 3.6% larger in Central American populations and 0.9% *smaller* in South American populations.

Size differences between the sexes associated with altitude and seasonality.—In all the tests discussed above, the 54 populations are regarded as consisting of two main groups—those with males larger and those with females larger. A contrasting point of view recognizes the two main groups as those with little or no size difference between the sexes, and those with marked difference in size between the sexes, regardless of whether the male or female is larger. In 24 of the 54 populations tested, the size difference between the sexes was significant at the 1% level (Table 1) and three others were barely outside this level. Including the three borderline populations with those having significant size dimorphism results in dividing the total of 54 equally, with an array of 27 that have sexual size difference and an equal number with little or no such difference. The samples were used for a 2×2 test of independence.

Of the 27 species having similar-sized sexes, 12 are limited to medium or high altitudes, whereas all but one of the species having sexual difference are essentially lowland dwellers. The correlation of upland habitat with lack of sexual difference in size is hence highly significant (Chi-square = 11.206). Of the 27 populations lacking sexual size difference, the 15 that are *not* montane are all essentially rain forest dwellers. The 27 populations having sexual size difference have 12 rain forest species, one montane species and 14 kinds that are characteristic of areas with a severe dry season. If the kinds characteristic of lowland rain forest and those characteristic of submontane forest and cloud forest are combined and arrayed against those in seasonally dry areas, there is again a highly

significant correlation between sexual size difference and seasonality of climate (Chi-square = 20.720).

Intraspecific variation.—In several instances two or more populations currently considered conspecific were sampled and compared. In the cases of *Anolis limifrons*, *Anolis humilis*, *Anolis lemurinus*, and *Anolis woodi*, supposed subspecies (*A. limifrons biscutiger*, *A. limifrons rodriguezi*, *A. lemurinus bourgaei*, *A. humilis uniformis*, *A. woodi attenuatus*, respectively) may actually be valid species. Only *Anolis cupreus* has geographic races whose status is clear-cut and unequivocal.

Four populations of *Anolis cupreus* were sampled: *A. c. cupreus* (Sardinal, Guanacaste Province, Costa Rica), *A. c. hoffmanni* (Cartago and San José, Costa Rica), *A. c. macrophallus* (Escuintla and vicinity, Guatemala) and *A. c. spilomelas* (Quepos, Puntarenas Province, Costa Rica). In these four populations the females averaged from 82.3% of male length (*macrophallus*) to 96.6% (*hoffmanni*). *A. c. macrophallus* and *A. c. spilomelas* are relatively large (49.6 mm at S-V) whereas *hoffmanni* is small (44.1) and *cupreus* is intermediate (47.4). Average male size is thus notably different in these subspecies (12% larger in *macrophallus* and *spilomelas* than in *hoffmanni*) whereas in females the corresponding difference is only 4%.

Sympatric species, competing most severely with anoles nearest their own size, may bring to bear selective pressure which influences the amount of sexual dimorphism in local populations of *A. cupreus*. *A. c. cupreus* at Sardinal is relatively free from such competition, but is sympatric with the relatively large, scarce and arboreal *Anolis pentaprion*. *A. c. spilomelas* and *A. c. macrophallus*, alike in having relatively large males and small females, both have sympatric abundant smaller species. For *spilomelas*, the smaller congener is *Anolis limifrons biscutiger* in which both sexes are much smaller than the male *spilomelas* and slightly smaller than the female. In the case of *macrophallus* the smaller species is *Anolis sericeus* in which the male is moderately smaller than the *macrophallus* male and the female is about the same size as the *macrophallus* female, not demonstrably larger or smaller. In *A. c. hoffmanni*, having sexes nearly alike in size, there is sympatry with *Anolis intermedius*, which has both sexes slightly larger than either sex of *hoffmanni*. It is noteworthy that the female of *A. c. hoffmanni* differs from females of the other three subspecies, which have white throats, in having some of the pinkish or orange color of the male dewlap. Although character displacement may be involved, the intraspecific trend, from marked sexual size difference in the lowland subspecies *cupreus*, *macrophallus*, and *spilomelas* to much less difference in the upland subspecies *hoffmanni*, parallels interspecific trends for the genus. *Anolis cupreus hoffmanni* inhabits upland, the Meseta Central of Costa Rica, where the annual cycle is characterized by a moderately

long and severe dry season but it is shorter and less severe than in the lowland habitats of the other three subspecies.

Four of the populations studied are tentatively assigned to *Anolis limifrons* and, if that assignment is correct, the species is notably variable in both size and sexual dimorphism. *A. l. biscutiger* from the Pacific lowlands of extreme southern Costa Rica, was named as a distinct species by Taylor (1956), combined with *A. limifrons* by Savage (1973) and treated as a subspecies by Fitch (1973a). It is seemingly isolated from other populations by the mountainous barrier of the continental divide. Its females are relatively large. *Anolis limifrons* (*limifrons*?) in Panama is several per cent larger than its counterpart in the Caribbean lowlands of Costa Rica, from which it differs also in having males slightly larger than females, and in having the dewlap yellow instead of dull white with a faint yellowish center. *Anolis limifrons rodriguezi* of the Yucatan Peninsula and northeastern Guatemala has sexes almost equal in size, has a yellow dewlap, and is about the same size as those of Panamanian populations but distinctly larger than those of Costa Rica. *Anolis rodriguezi* was considered a distinct species until Stuart (1948) allocated it to *Anolis limifrons* but it is noteworthy that Etheridge (1960), assigned it to a different species-series on the basis of anatomical characters.

In *Anolis humilis humilis* of Costa Rica, females are about 5% larger than males, but in *A. h. uniformis* the male is 2% larger and the dewlap has a central dark blue spot that is lacking in typical *humilis*. In *Anolis woodi attenuatus* both size and sexual dimorphism are several per cent greater than in *A. woodi woodi*, which has a pinkish or orange dewlap, in contrast to the dark brown of *A. w. attenuatus*. *Anolis lemurinus lemurinus* is several per cent larger than *A. l. bourgaei*, but sexual size difference is similar in both.

My findings have little bearing on the subspecific or specific status of the nine supposed subspecies but do suggest that the size relationship between the sexes is in delicate equilibrium and is readily altered by selection and subject to much geographic variation.

DISCUSSION

It is evident from the above account that selection has produced some populations with much sexual dimorphism and others with little or none at all, some with males larger than females, and others with the opposite size relationship between the sexes. It is here suggested that territorial habits, and especially development of polygyny, are among the conditions that favor selection of relatively large males, whereas need for intensified reproductive effort to produce larger offspring or to produce them more often, may favor selection of relatively large females. A trend toward monogamous

habits, or dependence on one type of prey within a narrow size range are conditions that might favor similar size in the sexes. All these factors and others, may exert their effects simultaneously, to varying degrees, producing the spectrum of variations in sexual dimorphism found in the genus *Anolis*.

Interspecific competition must have been a potent selective force in the evolution of existing anole species and populations, judging from extensive sympatry and the close similarities between species in their use of available resources. As many as seven species may occur together in one locality. The species that have extensive geographic ranges may have sympatry with a much larger number, and in the course of their evolution they must have interacted with even more species.

Every case of co-occurrence involves potential competition. It may be trivial in the most divergent species, especially if geographic overlap is slight, but there are all degrees of geographical and ecological overlap, and often there must be intense competition for resources. As a general rule, size of prey is proportional to size of anole; therefore similar-sized species compete most, and divergence in size, as by character displacement, alleviates competition.

A few kinds are so divergent from the matrix of mainland species in marginal distribution and/or specialized habitat, that they must be relatively free from interspecific competition. Certain parallels may be expected between those relatively isolated mainland species and various West Indian species that live in isolation on islands. In the latter, strong sexual dimorphism is the rule, with males much larger than females.

An outstanding example of an isolated mainland species is *Anolis carolinensis*. With an "Austroriparian" distribution in the southeastern United States, it is free from the competition of sympatric species except near Miami, Florida, and in Cuba and neighboring islands where it also occurs. In *A. carolinensis* of the southern United States female-to-male ratio is 79.0% with greater dimorphism than in other mainland species sampled, except *cuprinus* (73.46%) and *subocularis* (76.08%).

A. cuprinus and *A. subocularis* are also relatively isolated from the matrix of mainland tropical species, as both occur on the margins of the range of the genus in xeric regions in Mexico that are near the tolerance limits of anoles. However, both have sympatric congeners. *A. subocularis*, with a fairly extensive range in southern Guerrero, overlaps *A. gadovii* and *A. taylori*, each, insofar as known, confined to a single locality. Also, *A. subocularis* overlaps the smaller, wide-ranging *A. nebulosus*, but the latter occurs mostly farther north and at higher altitudes. *A. cuprinus* is limited to a small area near Zanatepec in southeastern Oaxaca, which it shares with the much more euryecic and more widespread but smaller, *A. sericeus*. In such cases, involving the co-occurrence of one species

confined to a small area and a second species which is wide-ranging (e.g. *cuprinus* and *sericeus*, *taylori* and *subocularis*, *gadovii* and *subocularis*), the selective pressure generated by competition in sympatry must be of trivial importance in its effect on the gene pool of the wide-ranging species even though its intensity locally may render it paramount in the ecology of the localized species. Hence, character displacement resulting from competition in sympatry may be unilateral, or at least it may affect one of the species involved much more than the other.

Actually, the mutual competition between any pair of overlapping species would rarely be the same for both. Besides having different proportions of their ranges sympatric, they would be subject to the following differential effects. (1) Size; the larger species would tend to dominate and displace the smaller one without being comparably affected. (2) Population density; the more abundant species in the area of overlap would exert the greater effect on its competitor. (3) Breadth of habitat; a species specialized for a particular structural niche within its habitat would be more affected by a competitor there than would a euryecic associate having the capacity for spatial or behavioral accommodation to exploit unutilized resources, as well as the capacity to exert competitive pressure.

It is conceivable that a pair of syntopic competitors might respond altogether differently to their mutual selective pressures, one evolving on a course of divergence while the other tends toward convergence. Cody (1968) has illustrated competitive convergence in bird songs. Sympatric, competing bird species may have evolved similar songs that function to maintain the integrity of territories both intraspecifically and interspecifically. In anoles the dewlap display fulfills the same function of territorial spacing. It is a general rule that sympatric anole species have strikingly different dewlaps. However, interspecific displays occur in nature and can be readily induced in confinement, and in some instances dewlaps that differ in detail are alike in general appearance. One such instance of resemblance is that between *Anolis sericeus* and *A. humilis uniformis*, which are different in most respects though both are Betas of the *Chrysolepis* species series. They are similar in size and have a red or orange dewlap with a central blue spot, and their ranges are partly sympatric. The actual displays of anoles are stereotyped and species-specific but they are too little known to permit statements as to whether they show divergence or convergence in competing kinds.

Size relationships between species, and their effects on competitive relationships, are complex, especially when more than two species occur together. Even if there are only two, various possibilities exist, for example: (1) A is larger. (2) B is larger. (3) A is bracketed by B which has one sex (either male or female) larger than either sex of A and the other smaller. (4) Male of A is larger than male of B, which is larger than female of A, which is larger

than female of B (or the sequence may be reversed, with the females of each species larger than the males).

Accompanying size differences between the sexes or replacing them in alleviating competition, there may be behavioral differences such as those pertaining to "structural niche," which includes diameter and height above ground of the perch used (Schoener, 1967, 1968; Schoener and Schoener, 1971a, 1971b; Keister, Gorman and Arroyo, 1975).

Several writers have noted size differences in the sexes of West Indian anoles, but no survey of such differences has as yet been made and few actual figures are available. In a study of Lesser Antillean Anoles, Lazell (1972) published several plates comparing the sexes in 21 kinds, including both species and subspecies. Strong sexual dimorphism in all kinds is indicated, with differences in pattern, coloration, display organs, body proportions and, especially, size. The plates presumably show typical size differences between the sexes in each kind and in every instance the male was larger, with females ranging from 60% to 97% of male length, averaging 72.3%. This mean is well below the minimum figure for the 54 mainland populations included in the present study.

All the anoles in Lazell's study were in the Alpha section of the genus in a species-group not represented in my study, so trends may have been influenced by phylogenetic relationships. The Lesser Antilles are all relatively small islands, and usually there are only one or two anole species to an island. Hence, there is, in general, little competition from associated slightly larger or smaller species, that might exert selective pressure against divergence in sizes of the sexes in a more complex fauna. Also, these islands are subject to pronounced seasonal change, with a breeding season alternating with a season of drought. As in mainland species, sexual size differences are probably strongly correlated with seasonally concentrated reproductive activity.

Year-round reproduction is characteristic of anole species that inhabit cloud forests or rain forests in a humid climate subject to little seasonal change (Fitch, 1972). However, in climates with well defined seasonal change, notably those with a severe dry season, reproduction is limited to the more favorable part of the year, which constitutes a distinct breeding season. Licht and Gorman (1970) found strong correlation between egg production and rainfall in Caribbean anoles. Egg production tended to decline with the advent of the dry season and to increase abruptly with the beginning of the rainy season. Species studied included *Anolis conspersus*, *A. cybotes*, *A. grahmi*, *A. lineatopus*, *A. richardi griseus*, *A. sagrei*, and *A. trinitatis* on the islands of Grand Cayman, Hispaniola, Jamaica and St. Vincent. In each population studied there was found to be at least some gamete production, in one or both sexes, throughout the year.

In the relatively stable cloud forest and rain forest environments, population structure and population density are also relatively stable, with reproduction, growth, and population turnover evenly distributed through the annual cycle. In contrast, seasonally dry habitats subject their anole inhabitants to environmental stresses that alternate with intraspecific stresses in more favorable parts of the year. At the onset of the breeding season the population consists essentially of adults (largely the recently matured young of the previous breeding season); hence, competition is intense for food and space and especially for mates. Under such conditions selection presumably would favor relatively large and aggressive males with highly developed display organs and display behavior.

CONCLUSIONS

Size relationships between the sexes were investigated in 54 populations of mainland anoles, from North America, Central America and South America, representing at least 45 full species. In most there was some difference between the sexes, with females varying from means as little as 73.5% of male length to means as much as 125.4% in different populations, forming almost a continuum. However, there were more species having the male larger than having the female larger, and there were more species having the sexes nearly the same size than with one sex much larger than the other.

Relatively isolated or marginal populations had significantly different sized sexes more often than did populations that were central and widely sympatric. Large size of the male dewlap was also positively correlated with sexual size difference in favor of the male. Alpha anoles had relatively large males more often than Betas.

Montane species were found to have the sexes similar in size (in 11 of 12), and this same tendency was found, though less strongly developed, in the species that live in tropical rain forest. In contrast, species living in seasonally dry climates, and having relatively short and concentrated breeding seasons, all had males relatively large compared with females. Seemingly, the intensified competition for mates and territory imposed by a concentrated breeding season has favored selection of relatively large males.

ACKNOWLEDGMENTS

Most of the data in this report was gathered in the field. My companions, who were active in capturing anoles and gathering data, include Alice Fitch Echelle, Anthony A. Echelle, Chester W. Fitch, David C. Fitch, Virginia R. Fitch, Robert W. Henderson and Richard K. La Val. Robert C. Waltner performed many of the biometrical tests. Richard F. Johnston, Gunther Schlager and Norman A. Slade provided guidance in applying appropriate statistical

tests to the data. Financial support from the University of Kansas (General Research Grant #3344-5038) and the National Science Foundation (GB 6724) is gratefully acknowledged.

LITERATURE CITED

- CODY, M. L. 1968. On the method of resource division in grassland bird communities. *Amer. Naturalist*, 102:107-147.
- ETHERIDGE, R. E. 1960. The relationships of the Anoles (Reptilia: Sauria: Iguanidae): an interpretation based on skeletal morphology. Ph.D. Dissertation, University of Michigan, 236 pp.
- EVANS, L. T. 1965. Social behavior. Introduction in *Lizard Ecology. A Symposium*. University of Missouri Press, Columbia, Missouri.
- FITCH, H. S. 1956. An ecological study of the Collared lizard (*Crotaphytus collaris*). *Univ. Kansas Publ. Mus. Nat. Hist.*, 8:213-274.
- FITCH, H. S., 1972. Ecology of *Anolis tropidolepis* in Costa Rican cloud forest. *Herpetologica*, 28:10-21.
- FITCH, H. S. 1973a. Observations on the population ecology of the Central American iguanid lizard, *Anolis cupreus*. *Caribbean Jour. Sci.*, 13:215-230.
- FITCH, H. S. 1973b. Population structure and survivorship in some Costa Rican lizards. *Occas. Papers Univ. Kansas Mus. Nat. Hist.*, no. 18:18-41.
- FITCH, H. S. 1973c. A field study of Costa Rican lizards. *Univ. Kansas Sci. Bull.*, 50:39-126.
- FITCH, H. S., ECHELLE, A. A., ECHELLE, A. F. 1972. Variation in the Central American iguanid lizard *Anolis cupreus* with the description of a new subspecies. *Occas. Papers Univ. Kansas Mus. Nat. Hist.*, no. 8:1-20.
- KEISTER, A. R., GORMAN, G. C., ARROYO, D. C. 1975. Habitat selection behavior of three species of *Anolis* lizards. *Ecology*, 56:220-225.
- LAZELL, J. D. JR. 1972. The anoles (Sauria, Iguanidae) of the Lesser Antilles. *Bull. Mus. Comp. Zool. Harvard*, 143:1-115.
- LICHT, P., GORMAN, G. C. 1970. Reproductive and fat cycles in Caribbean *Anolis* lizards. *Univ. California Publ. Zool.*, 95:1-52.
- SAVAGE, J. M. 1973. A preliminary handlist of the herpetofauna of Costa Rica. *Univ. S. California*, Los Angeles, 17 pp.
- SCHOENER, T. 1967. The ecological significance of sexual dimorphism in size in the lizard *Anolis conspersus*. *Science*, 155:474-477.
- SCHOENER, T. 1968. The *Anolis* lizards of Bimini: resource partitioning in a complex fauna. *Ecology*, 49:704-726.
- SCHOENER, T., SCHOENER, A. 1971a. Structural habitats of West Indian *Anolis* lizards. I. Jamaican lowlands. *Breviora*, 368:1-53.
- SCHOENER, T., SCHOENER, A. 1971b. Structural habitats of West Indian *Anolis* lizards. II. Puerto Rican lowlands. *Breviora*, 375:1-39.
- SOKOL, R. R., ROHLF, F. J. 1969. *Biometry. The Principles and Practice of Statistics in Biological Research*. W. H. Freeman and Co., San Francisco. 776 pp.
- STUART, L. C. 1948. The amphibians and reptiles of Alta Verapaz, Guatemala. *Misc. Publ. Mus. Zool. Univ. Michigan*, 69:1-109.
- TAYLOR, E. H. 1956. A review of the lizards of Costa Rica. *Univ. Kansas Sci. Bull.* 38, pt. 1:1-322.
- WILLIAMS, E. E. 1969. The ecology of colonization as seen in the zoogeography of anoline lizards on small islands. *Quart. Rev. Biol.* 44:345-389.

APPENDIX 1

Series of *Anolis* measured alive in the field and released
(or measured when freshly killed, before preservation).

<i>aquaticus</i>	Costa Rica, Puntarenas Pr., Finca Las Cruces near San Vito. Feb. and Mar.
<i>attenuatus</i>	Costa Rica, Puntarenas Pr., Monteverde. Jan., Feb., Mar., July, Aug., Sept., Oct., Dec.
<i>biscutiger</i>	Costa Rica, Puntarenas Pr., Quepos. Jan., Mar., Apr., May, June, July, Aug., Sept., Dec.
<i>bourgaei</i>	Guatemala, Izabal Pr., Puerto Barrios. Feb.
<i>carpenteri</i>	Costa Rica, Cartago Pr., Turrialba. Mar. Costa Rica, Heredia Pr., Finca La Selva. Feb., Apr., Aug., Oct., Nov.
<i>cupreus</i>	Costa Rica, Guanacaste Pr., Sardinal. Feb., Mar., May, June, July, Aug. Costa Rica, Puntarenas Pr., Quepos. Jan., Mar., Apr., May, June, July, Aug., Sept., Dec. Costa Rica, San José Pr., San José, and Cartago Pr., Cartago. Mar., Apr., May, June, Aug., Sept.
<i>cuprinus</i>	Guatemala, Escuintla Pr., 6 mi. E Escuintla, El Salto. Mar.
<i>dollfusianus</i>	Mexico, Oaxaca Pr., 7 km E Zanatepec. Feb. Mexico, Chiapas Pr., 14 km N Tapachula. Feb. Guatemala, Escuintla Pr., Retalhuleu. Feb.
<i>gadovii</i>	Mexico, Guerrero Pr., Tierra Colorada. May, June, July.
<i>gemmosus</i>	Ecuador, Pichincha Pr., Tandapi. Late Feb.
<i>humilis</i>	Costa Rica, Limón Pr., Beverly. Year-round. Costa Rica, Alajuela Pr., San Miguel de Sarapiquí. Jan., Feb., Mar., Apr., May, June, Aug.
<i>intermedius</i>	Costa Rica, Cartago Pr., Cartago and San José Pr., San José. Year-round.
<i>lemurinus</i>	Mexico, southern Chiapas Pr., various localities. Guatemala, Escuintla and Retalhuleu Pr., various localities. Feb. and Mar.
<i>limifrons</i>	Costa Rica, Cartago Pr., Turrialba. Year-round.
<i>nigrolineatus</i>	Ecuador, El Oro Pr., 5 km E Machala. 11-12 Mar.
<i>peraccae</i>	Ecuador, Pichincha Pr., 5 km E., 16 km E., and 22 km E., Santo Domingo des los Colorados; Estación Biológica Río Palenque. Late Feb. and early Mar.
<i>polylepis</i>	Costa Rica, Puntarenas Pr., Finca Las Cruces near San Vito. Feb. and Mar.
<i>sericeus</i>	Mexico, Chiapas Pr., 14 km N, and 16 km S Tapachula; 12.1 km W Arriaga. Guatemala, Escuintla Pr., 6 km S Escuintla. Feb. and Mar.
<i>subocularis</i>	Mexico, Guerrero Pr., 1 mi. N. Cruz Grande, Oaxaca Pr., Guachupin, 8 km ESE Río Grande, 7.5 km W La Estancia, 12.5 km ESE Marquelia, 30 km and 7.7 km ESE San Marcos. Feb. and July.
<i>taylori</i>	Mexico, Guerrero Pr., 5 mi S Las Cruces near Acapulco, Puerto Marqués. Feb., Mar., May, June, July.
<i>tropidolepis</i>	Costa Rica, Alajuela Pr., Hacienda El Prado. Year-round.
<i>tropidonotus</i>	Mexico, Oaxaca, 5 mi. N Jucatepec. Feb.

Series of preserved specimens of *Anolis* measured in
University of Kansas Museum of Natural History.

<i>aequatorialis</i>	Ecuador, Pichincha Pr., Tandapi. Feb.
<i>auratus</i>	Panama, Canal Zone, Coclé, Colón, Panama. Various localities and dates.
<i>biporcatus</i>	Guatemala, Alta Verapaz and El Petén Pr. Costa Rica, Cartago, Guanacaste, Heredia and Limón Pr. Panama, Bocas del Toro and San Blas Pr. and Canal Zone. Various localities and dates.
<i>capito</i>	Costa Rica, Alajuela, Heredia and Limón Pr. Panama, Bocas del Toro, Chiriquí and Darién Pr. Various localities and dates.
<i>carolinensis</i>	U.S.A., Alabama, Arkansas, Florida, Louisiana, Mississippi, and Texas. Various localities and dates.
<i>chrysolepis</i>	Ecuador, Napo Pr., Limón Cocha, Puerto Oro, Santa Cecilia. Feb., Mar., Apr., May, June, July, Aug., Sept., Oct., Nov.
<i>crassulus</i>	Mexico, Chiapas Pr. Guatemala, Huehuetenango, Quezaltenango, and Sololá Pr. Various localities and dates.
<i>damulus</i>	Mexico, Oaxaca Pr., Vista Hermosa, 8 km S Metla. Feb.
<i>dunni</i>	Mexico, Guerrero Pr., Agua de Obispo.
<i>frenatus</i>	Panama. Canal Zone, Darién Pr. Various localities and dates.
<i>fuscoauratus</i>	Ecuador, Napo Pr., Bermejo, Limón Cocha, Puerto Libre, Santa Cecilia. Feb., Mar., Apr., May, June, July, Oct., Nov., Dec.
<i>heteropholidotus</i>	El Salvador, Santa Ana Pr., Hacienda Montecristo, Metapán Mountains. Feb., July, Dec.
<i>kemptoni</i>	Panama, Chiriquí Pr., Finca Ojo de Agua, Finca Palosanto. Feb., Apr., July, Aug.
<i>limifrons</i>	Panama, Canal Zone, Colón, Darién and San Blas Pr. Various localities and dates.
<i>lionotus</i>	Costa Rica, Alajuela, Cartago, Guanacaste, Heredia, Limón, and San José Pr. Various localities and dates.
<i>megapholidotus</i>	Mexico, Oaxaca Pr. Various localities and dates.
<i>nebulosus</i>	Mexico, Chihuahua, Durango, Guerrero, Jalisco, Michoacán, Nayarit, Sinaloa, and Zacatecas Pr. Various localities and dates.
<i>ortoni</i>	Ecuador, Napo Pr., Bermejo. Brazil, Para Pr., Belém. Mar., Apr., June, July, Aug.
<i>pachypus</i>	Panama, Chiriquí Pr.
<i>pentaprion</i>	Mexico, Tabasco Pr. Costa Rica, Guanacaste and Puntarenas Pr. Panama, Canal Zone, Bocas del Toro and Panama Pr. Various localities and dates.
<i>poecilopus</i>	Panama, Darién Pr.
<i>punctatus</i>	Ecuador, Napo Pr.
<i>rodriguezi</i>	Mexico, Campeche, Quintana Roo and Yucatán Pr. Various localities. Feb., Mar., Apr., July.
<i>trachyderma</i>	Ecuador, Napo Pr., Puerto Libre, Santa Cecilia. Year-round.
<i>tropidogaster</i>	Panama, Darién Pr. El Real, Río Cupe, Río Tuira at Río Mono, Río Jaque. Apr., May, July, Oct.
<i>uniformis</i>	Guatemala, Alta Verapaz Pr., Chinajá, 3 km S Chinaja; El Petén Pr. 20 km NNW Chinajá, 11 km, and 15 km NW Sayaxché. Feb., Mar., June.
<i>vittigerus</i>	Panama, Darién Pr., Cana, Cerro Sapo, Cerro Cituro (north ridge), Río Jaque, Río Cupe, Río Tuira at Río Mono, Río Ucurgante. Jan., Apr., May, Nov.
<i>woodi</i>	Panama, Chiriquí Pr. Feb., May.

APPENDIX 2
Ecological, morphological and evolutionary groupings.

TABLE 3.—SIZE, COLORATION AND CONTRAST OF MALE DEWLAP.

	Two or More Colors	One Color	Dull
Large	<i>aequatorialis</i> <i>cupreus</i>	<i>carolinensis</i> <i>cuprinus</i> <i>dunni</i> <i>fuscoauratus</i> <i>kemptoni</i> <i>lionotus</i> <i>polylepis</i> <i>subocularis</i> <i>tropidogaster</i>	<i>attenuatus</i> <i>frenatus</i> <i>woodi</i>
Medium	<i>aquaticus</i> <i>chrysolepis</i> <i>humilis</i> <i>sericeus</i> <i>uniformis</i>	<i>carpenteri</i> <i>damulus</i> <i>dollfusianus</i> <i>heteropholidotus</i> <i>nebulosus</i> <i>petersi</i> <i>poecilopus</i> <i>punctatus</i> <i>rodriguezi</i> <i>tropidonotus</i>	<i>bourgaei</i> <i>lemurinus</i> <i>peraccae</i>
Small		<i>crassulus</i> <i>limifrons</i> <i>pachypus</i> <i>tropidolepis</i>	<i>biporcatus</i> <i>biscutiger</i> <i>capito</i> <i>intermedius</i> <i>limifrons</i> (Turrialba) <i>nigrolineatus</i> <i>trachyderma</i>

Female dewlap:

Relatively large:

aequatorialis, *biporcatus*, *chrysolepis*, *frenatus*, *gadovii*, *lemurinus*, *pentaptrion*, *vittigerus*.

Small:

attenuatus, *bourgaei*, *crassulus*, *dollfusianus*, *dunni*, *megapholidotus*, *nebulosus*, *petersi*, *poecilopus*, *punctatus*, *sericeus*, *subocularis*, *taylori*, *tropidonotus*, *woodi*.

Absent, chin colored:

carpenteri, *cupreus* (San José), *humilis*, *pachypus*, *tropidolepis*, *uniformis*.

Absent, chin plain:

aquaticus, *auratus*, *biscutiger*, *capito*, *carolinensis*, *cupreus*, *cuprinus*, *damulus*, *fuscoauratus*, *gemmosus*, *heteropholidotus*, *intermedius*, *kemptoni*, *limifrons* (Panama), *limifrons* (Turrialba), *lionotus*, *nigrolineatus*, *ortoni*, *peraccae*, *polylepis*, *rodriguezi*, *trachyderma*, *tropidogaster*.

Phylogeny

Alpha species series

Carolinensis Group:

carolinensis.

Latifrons Group:

frenatus, *gemmosus*, *nigrolineatus*, *peraccae*, *punctatus*, *ortoni*.

Beta species series

Chrysolepis Group:

aquaticus, *auratus*, *bourgaei*, *chrysolepis*, *cupreus*, *cuprinus*, *crassulus*, *damulus*, *dollfusianus*, *dunni*, *gadovii*, *heteropholidotus*, *humilis*, *intermedius*, *lemurinus*, *megapholidotus*, *nebulosus*, *pachypus*, *poecilopus*, *rodriguezi*, *sericeus*, *subocularis*, *taylori*, *tropidogaster*, *tropidolepis*, *tropidonotus*, *uniformis*, *vittigerus*, *woodi*.

Fuscoauratus Group:

biscutiger, *carpenteri*, *fuscoauratus*, *kemptoni*, *limifrons*, *lionotus*, *polylepis*.

Petersi Group:

biporcatus, *capito*, *pentaprion*, *petersi*.

Geography

North American:

carolinensis, *cuprinus*, *damulus*, *dunni*, *gadovii*, *megapholidotus*, *nebulosus*, *subocularis*, *taylori*.

Central American:

aquaticus, *attenuatus*, *biporcatus*, *biscutiger*, *bourgaei*, *capito*, *carpenteri*, *crassulus*, *cupreus*, *dollfusianus*, *frenatus*, *heteropholidotus*, *humilis*, *intermedius*, *kemptoni*, *lemurinus*, *limifrons* (Panama), *limifrons* (Turrialba), *lionotus*, *pachypus*, *pentaprion*, *petersi*, *polylepis*, *tropidolepis*, *tropidonotus*, *uniformis*, *woodi*.

South American:

aequatorialis, *auratus*, *chrysolepis*, *fuscoauratus*, *gemmosus*, *nigrolineatus*, *ortoni*, *peraccae*, *poecilopus*, *punctatus*, *trachyderma*, *tropidogaster*, *vittigerus*.

Habits

Highly arboreal:

biporcatus, *frenatus*, *pentaprion*, *petersi*, *punctatus*.

Trunk or low tree:

aequatorialis, *attenuatus*, *bourgaei*, *capito*, *carolinensis*, *carpenteri*, *fuscoauratus*, *gemmosus*, *intermedius*, *lemurinus*, *nigrolineatus*, *woodi*.

Tree-trunk-to-ground:

biscutiger, *cupreus*, *cuprinus*, *damulus*, *dollfusianus*, *dunni*, *heteropholidotus*, *kemptoni*, *limifrons* (Panama), *limifrons*, (Turrialba), *nebulosus*, *ortoni*, *pachypus*, *polylepis*, *rodriguezi*, *sericeus*, *subocularis*, *tropidolepis*, *tropidogaster*, *vittigerus*.

Ground level:

aquaticus, *auratus*, *chrysolepis*, *crassulus*, *gadovii*, *humilis*, *lionotus*, *megapholidotus*, *poecilopus*, *taylori*, *trachyderma*, *tropidonotus*, *uniformis*.

Female size ranked from largest to smallest:

frenatus, *petersi*, *capito*, *biporcatus*, *attenuatus*, *aequatorialis*, *chrysolepis*, *punctatus*, *woodi*, *lemurinus*, *vittigerus*, *gadovii*, *poecilopus*, *lionotus*, *pentaprion*, *aquaticus*, *gemmosus*, *taylori*, *bourgaei*, *heteropholidotus*, *trachyderma*, *kemptoni*, *tropidolepis*, *tropidogaster*, *nigrolineatus*, *damulus*, *polylepis*, *carolinensis*, *auratus*, *cuprinus*, *peraccae*, *pachypus*, *intermedius*, *fuscoauratus*, *ortoni*, *dunni*, *megapholidotus*, *limifrons* (Panama), *rodriguezi*, *crassulus*, *cupreus*, *tropidonotus*, *nebulosus*, *cupreus* (Quepos), *cupreus* (Sardinal), *sericeus*, *carpenteri*, *cupreus* (Guatemala), *biscutiger*, *subocularis*, *limifrons* (Turrialba), *humilis*, *dollfusianus*, *uniformis*.

Syntopy:

Widespread and dominant:

auratus, *biporcatus*, *biscutiger*, *bourgaei*, *crassulus*, *capito*, *chrysolepis*,

cupreus (4 populations), *frenatus*, *fuscoauratus*, *humilis*, *intermedius*, *lemurinus*, *limifrons* (Turrialba), *limifrons* (Panama), *lionotus*, *nebulosus*, *ortoni*, *pentaprion*, *petersi*, *punctatus*, *rodriguezi*, *trachyderma*, *tropidogaster*, *tropidolepis*, *tropidonotus*, *uniformis*, *woodi*.

Restricted in range and dominated:

aequatorialis, *aquaticus*, *attenuatus*, *carpenteri*, *damulus*, *dollfusianus*, *gemmosus*, *heteropholidotus*, *kemptoni*, *nigrolineatus*, *pachypus*, *peraccae*, *polylepis*.

Marginal:

carolinensis, *cuprinus*, *dummi*, *gadovii*, *megapholidotus*, *nebulosus*, *sericeus*, *subocularis*, *taylori*.

Type of climate

Severely seasonal:

carolinensis, *cupreus* (4 populations), *cuprinus*, *dollfusianus*, *gadovii*, *lionotus*, *nigrolineatus*, *pentaprion*, *sericeus*, *subocularis*, *taylori*.

Relatively aseasonal:

Montane and cloud forest:

attenuatus, *crassulus*, *damulus*, *dummi*, *heteropholidotus*, *intermedius*, *kemptoni*, *megapholidotus*, *nebulosus*, *pachypus*, *petersi*, *tropidolepis*.

Lowland rain forest:

aequatorialis, *aquaticus*, *auratus*, *biporcatus*, *bourgaei*, *capito*, *carpenteri*, *chrysoplepis*, *frenatus*, *fuscoauratus*, *gemmosus*, *humilis*, *lemurinus*, *limifrons* (Panama), *limifrons* (Turrialba), *ortoni*, *peraccae*, *poecilopus*, *polylepis*, *punctatus*, *rodriguezi*, *trachyderma*, *tropidogaster*, *tropidonotus*, *uniformis*, *vittigerus*.

UNIVERSITY OF KANSAS PUBLICATIONS

MUSEUM OF NATURAL HISTORY

The University of Kansas Publications, Museum of Natural History, beginning with volume 1 in 1946, was discontinued with volume 20 in 1971. Shorter research papers formerly published in the above series are now published as Occasional Papers, Museum of Natural History. The Miscellaneous Publications, Museum of Natural History, began with number 1 in 1946. Longer research papers are published in that series. Monographs of the Museum of Natural History were initiated in 1970. All manuscripts are subject to critical review by intra- and extramural specialists; final acceptance is at the discretion of the publications committee.

Institutional libraries interested in exchanging publications may obtain the Occasional Papers and Miscellaneous Publications by addressing the Exchange Librarian, University of Kansas Library, Lawrence, Kansas 66045. Individuals may purchase separate numbers of all series. Prices may be obtained upon request addressed to Publications Secretary, Museum of Natural History, University of Kansas, Lawrence, Kansas 66045.

Editor: RICHARD F. JOHNSTON

PRINTED BY
UNIVERSITY OF KANSAS PRINTING SERVICE
LAWRENCE, KANSAS

Date Due

~~APR 30 1983~~

Acme

Bookbinding Co., Inc.
300 Summer Street
Boston, Mass. 02210



3 2044 093 361 665

